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# Variations in modern pollen distribution in sediments from nearby upland lakes: implications for the interpretation of paleoecological data

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## ABSTRACT

To determine whether modern pollen content in sediments from upland lake systems reflects the factual regional and extra-local vegetation composition, we analysed twenty-five samples focusing on aspects such as pond size and morphology, relative position in the catchment, local vegetation, canopy configuration and seasonality of the water table. The average pollen percentages of all sediment samples studied allows a fairly good reconstruction of the main vegetation units in the area, but major differences between the average samples obtained in each sedimentary system, and also between some samples taken from the same system are found. The main factors explaining those differences are the size of the pond, its tree canopy and the seasonality of the water table, which strongly determines the Ericaceae and *Pinus* percentages. A high-resolution multiproxy palaeoecological record from a small upland lake is re-evaluated in light of the new experimental evidence, and it is concluded that the interpretation of the importance of heathland and pinewoods in the Late Glacial landscape using pollen data may be magnified by the transport of both pollen types through water flows and their accumulation in the basin. Furthermore, anomalous *Pinus* pollen peaks occur in dry periods when the water table remains low. The sediment can also be depleted of some high-buoyancy pollen types (tetrads and saccate) when the water level is high and effluents are active. These effects may also be important in fluvio-marine systems in which Ericaceae and *Pinus* pollen are often overrepresented.

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## 1. Introduction

Pollen assemblages obtained from modern sediment samples are an essential source of information for interpreting the fossil pollen records and understanding their environmental implications. Furthermore, because pollen analysis can be used to reconstruct ancient climates and environments, calibration between modern and past pollen data allows to model and predict the consequences of current climate change. It is therefore indispensable to explore the relationship between current vegetation and pollen records, and during the last few decades the development of image analysis and land cover techniques have enabled a more coherent linkage between pollen assemblages and variety of landscape scenarios (e.g. Bunting et al., 2004; Räsänen et al., 2007; Githumbi et al., 2022).

Modern pollen databases provide pollen surface samples to support studies of land cover and past climate using fossil pollen (Davis et al., 2020). Particularly, modern samples are used in quantitative climate and land cover reconstructions as training sets for calibration and,

ultimately, to establish and model the relationship between vegetation and pollen assemblages (based on the different pollen productivity of each taxa) in order to provide quantitative estimates of past vegetation landscape composition from fossil pollen records (e.g. Davis, 1963; Davis et al., 1973; Davis and Webb, 1975; Nakagawa et al., 2002; Chevalier et al., 2020). Modern pollen evidence can also be ideally linked to several types of well-documented natural or human-induced environmental processes (climate change, fires, pests, diseases, edaphic and hydrosere changes, deforestation, afforestation, cultivation, etc.) in order to study their effects on vegetation, land use and land cover. Therefore, pollen assemblages from modern sediment help to improve the value of fossil pollen records as spatially resolved data for reconstructing vegetation and climate changes that have occurred during the Quaternary (Davis et al., 2020).

Most often, pollen data in modern sediment samples are obtained from moss polsters or anaerobic systems such as the surface layers (<100–150 yr old) of lake, bog and fluvio-marine sediments. Studies of this type also help to understand pollen productivities (e.g. Broström et al., 2004; Duffin and Bunting, 2008) and taphonomic problems with regard to pollen transport, deposition and preservation (e.g. DeBusk, 1997; Seppä et al., 2004; Brown et al., 2007; Xu et al., 2012; Qin et al.,

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2015; García-Moreiras et al., 2015). Some palynologists stress the importance of studying modern pollen in lake surface sediments as calibration models, because it is from lake sediment samples that much of the fossil pollen is extracted (Seppä et al., 2004; Qin et al., 2015). The pollen records of lake sediments come from allochthonous material and from indigenous material that occurs in the lake (Bradley, 2015). Allochthonous material comes mainly from aerial and aquatic inputs, and aquatic pollen comes from groundwater flows, runoff and fluvial flows (Xu et al., 2012). The study of these processes reveals the dispersal capacity of the pollen of different species, their productivity and their abundance in the communities, thus improving the interpretation of the sedimentary sequences (e.g. Lozano-García et al., 2014).

Pollen percentages are not linearly related to the vegetation but are affected by variables such as pollen production, and the size and type of the sedimentation basin (Jacobson and Bradshaw, 1981; Sugita, 1994; Hicks et al., 2001). Thus, models have been developed to predict the vegetation. Within the landscape reconstruction algorithm (LRA), the REVEALS model (Sugita, 2007a) predicting the regional vegetation cover is based on sedimentary pollen counts from large lakes, and it is ideal for predicting the main elements of the vegetation of large areas. Alternatively, the LOVE model is designed to reconstruct the vegetation of smaller areas from pollen records in smaller sedimentary deposits (Sugita, 2007b). Because the application of the LRA needs good-quality information on pollen productivity and dispersion, other alternatives have been developed, such as the MARCO POLO model (Mrotzek et al., 2017), which uses only pollen count values and not pollen dispersal ability. Most models considering pollen dispersal are based on Gaussian plume models, but Theuerkauf et al. (2016) showed that REVEALS performed better applying Lagrangian stochastic models. However, it should be noted that these models are not designed for use in places that receive significant fluvial pollen input (Theuerkauf et al., 2016).

Khomutova (1995) reports that, in general, aquatic species have a much lower pollen production than terrestrial species, as well as a thinner exine, which also facilitates their degradation. They are therefore commonly underrepresented in lake sediments. Xu et al. (2012) indicate that only 12% of the pollen that reaches the large Baiyangdian Lake does so by air, the remaining 88% being provided by the water flows; and this figure increases to 92% if local hydrophytic species are excluded. In the central Tibetan Plateau Li (2019) found that 90.5% of the pollen collected in the lakes studied came from regional vegetation, and only 9.5% came from herbaceous ecosystems in the surroundings of the sedimentary system. Therefore, lacustrine sediments can be used as a reference to reconstruct the regional vegetation of the basin. However, in regions lacking large lakes, such as the NW Iberian Peninsula (Fig. 1a), most of the pollen data come from valley bottoms or small basins of glacial origin. Many of these sites began as small lakes with oscillating water tables that subsequently underwent paludification (e.g. Muñoz Sobrino et al., 1997, 2001, 2004, 2012a, 2013; Morales-Molino and García-Antón, 2014; Iriarte-Chiapusso et al., 2016; Sánchez-Morales et al., 2022).

The behaviour of some species with high pollen productivity, such as pines (e.g. Desprat et al., 2015), requires detailed studies to be able to accurately evaluate their dynamics in lakes (e.g. Davis, 1963; Jensen et al., 2002; Muñoz Sobrino et al., 2012a, 2013; Rull et al., 2021), coastal lagoons (e.g. Stutz and Prieto, 2003; Rodríguez-Gallego et al., 2012; Azuara et al., 2019; Gómez-Orellana et al., 2021) and shallow fluvio-marine deposits (e.g. García-Moreiras et al., 2015; Liénart et al., 2022). Dai et al. (2014) report that coastal marine sediments have a high concentration of pine pollen, most of which may come from river rather than windblown inputs (Beaudouin et al., 2007). This trend also occurs in fluvio-marine contexts such as the flooded coastal valleys (rias) of the NW Iberian Peninsula (e.g. Muñoz Sobrino et al., 2007, 2012b, 2014, 2016; García-Moreiras et al., 2015, 2018).

In order to objectively assess this and other possible local effects (site size, tree canopy and hydric regime) in modern and fossil pollen

assemblages, it may be useful to evaluate the modern accumulation of pine pollen in relation to other deciduous and shrubby formations, as recorded in a series of small ponds with different characteristics located along the same drainage basin. The ponds selected for this study are located in a geographically small space (Fig. 1b) but also have a series of differentiating characteristics that could influence each local pollen fingerprint. Thus, it is intended, first, to evaluate the relationship between the pollen content of the sediment collected in different lacustrine deposits distributed throughout the same continental sub-basin (Fig. 1b) and the local (water-dependent), extra-local (within a radius of 500 m) and regional (within a radius of 2000 m) vegetation surrounding them; and, second, to determine whether this relationship can vary according to the specific conditions of each sedimentary deposit, including aspects such as their particular morphologies, their sizes, the uneven tree canopy that surrounds or covers them, their position along the basin and the seasonality of their water tables. In addition, the applicability of the results of these analyses is tested by comparing them with the multiproxy data available on a small lake with an oscillating water table located in an upland mountain area in the NW Iberian Peninsula: Laguna de la Roya (LR in Fig. 1, Muñoz Sobrino et al., 2013). Thus, the new experimental evidence also offers new perspectives for re-evaluating the palaeoecological meaning of some pollen evidence recorded in this small lake during the period between the Late Glacial and the Early Holocene.

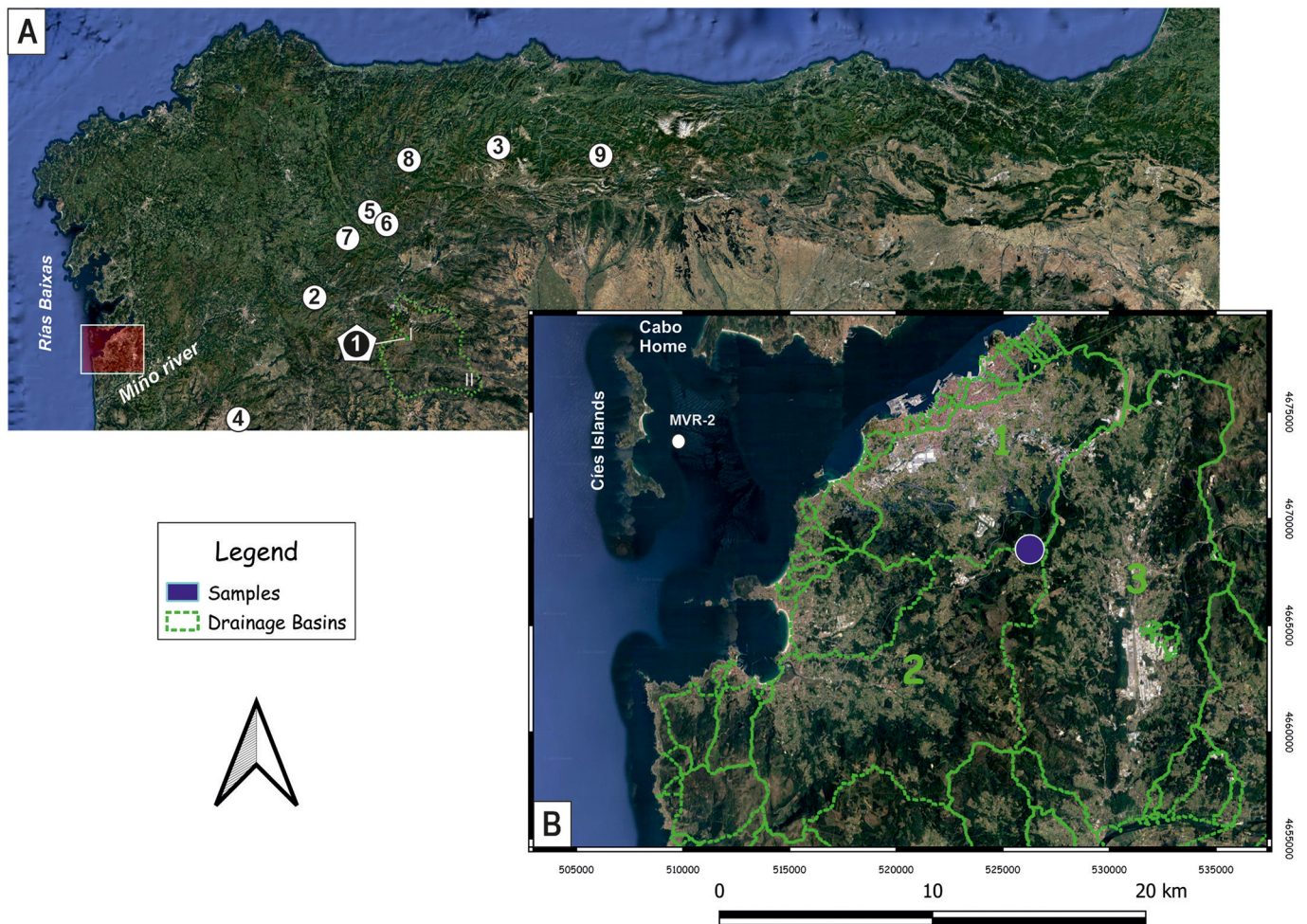
## 2. Study area

The Rías Baixas in NW Iberia (Fig. 1) is a coastal area of undulating relief where low and medium altitude elevations, mainly N-S oriented, alternate with small depressions (Fig. 1b), and the main coastal watersheds end in several major non-glaciated flooded fluvio-marine systems (rias). The predominant substrate is of granitic origin, with abundant acid metamorphic rocks. The climate is temperate with a slight Mediterranean tendency (Rodríguez Guitián and Ramil-Rego, 2007). The average annual temperature is 13.4°C, average relative humidity 77.3%, total annual rainfall 1864.3 mm, and monthly average rainfall 155.4 mm. However, the monthly rainfall between May and September 2019 (when the pond samples were taken) was only 44.4 mm/month, whereas for the rest of the year it was 234.6 mm/month (MeteoGalicia, 2021).

Biogeographically, the Rías Baixas subsector (Fig. 1) belongs to the European Atlantic Province, included in the Atlantic-European Subregion of the Eurosiberian Region (Rodríguez Guitián and Ramil-Rego, 2008), within the thermotemperate and mesotemperate bioclimatic belts (Rodríguez Guitián and Ramil-Rego, 2007). The characteristic vegetation of this bioregion is made up of a variety of species, including *Acer pseudoplatanus* L., *Betula pubescens* Ehrh., *Daboecia cantabrica* (Huds.) K. Koch, *Frangula alnus* Mill., *Fraxinus excelsior* L., *Hypericum androsaemum* L., *Ilex aquifolium* L., *Arbutus unedo* L., *Laurus nobilis* L., *Glandora prostrata* (Loisel.) DC Thomas, *Prunus padus* L., *Quercus suber* L., *Quercus robur* L., *Rosa villosa* L., *Salix alba* L., *Salix caprea* L., *Sorbus aucuparia* L., *Ulex europaeus* L., *Ulex minor* Roth, *Ulmus glabra* Huds. and *Castanea sativa* Mill.

## 3. The sedimentary systems

All the sedimentary systems considered in the first part of this study, a set of three ponds and also the drainage channel of one of them (Fig. 2), are located in the As Lagoas-Marcosende Campus of the Universidade de Vigo (Fig. 2), in the main basin of the Ría de Vigo (Fig. 1b). Much of the vegetation located around the campus was artificially introduced through the Marcosende Campus Revegetation Plan, a corrective measure carried out in the late 1990s after the felling of the plantations of pine (*Pinus pinaster* Aiton) that occupied the entire area. The introduced species were native trees and shrubs, including *Quercus* spp., *Prunus* spp., *Fraxinus* spp., *Tilia* spp., *Castanea sativa* Mill., *Corylus*



**Fig. 1.** a) NW Iberia: situation of the experimental study area in the Rías Baixas and localization of 1. LR: Laguna de la Roya (Allen et al., 1996; Muñoz Sobrino et al., 2013) and other pollen sites discussed in the text: 2. Arroyo de As Lamas (Maldonado Ruíz, 1994); 3. Lago de Ajo (Allen et al., 1996); 4. Lagoa de Marinho (Ramil-Rego et al., 1998); 5. Porto Ancares (Muñoz Sobrino et al., 1997); 6. A Golada (Muñoz Sobrino et al., 1997); 7. Lagoa de Lucenza (Muñoz Sobrino et al., 2001); 8. Pena Velosa (Muñoz Sobrino et al., 2012a); 9. Lago Ausente (Morales-Molino et al., 2022). The total local catchment of Laguna de la Roya (I) is 0.21 km<sup>2</sup>, while the complete Sanabria sub-basin (II) is about 502.45 km<sup>2</sup>. b) Southern margin of the Ría de Vigo (NW Iberia), with the limits of the main sub-basins and the situation of the samples used for the experimental study and the pollen site MVR-2 (Muñoz Sobrino et al., 2016): 1. Lagares river basin (72,85 km<sup>2</sup>); 2. Miñor river basin (101,31 km<sup>2</sup>); 3. Louro river basin (155,99 km<sup>2</sup>).

*avellana* L., *Sambucus nigra* L., *Arbutus unedo* L. and *Acer pseudoplatanus* L. (OMA, 2020). However, in the surroundings of the campus there are still forest plantations of *Pinus pinaster* Aiton and *Eucalyptus globulus* Labill., as well as remains of native vegetation, which includes mixed deciduous forests, oak groves, cork oak groves, shrubs (mainly Fabaceae) and heaths (Ericaceae).

Ponds P (Philology), S (Science) and L (Laws), sorted by decreasing sizes, are located on the main watershed at the southern margin of the Ría de Vigo belonging to the Galician coast basin. However, the entire basin can be subdivided into three main sub-basins in the highlands and multiple smaller sub-basins close to the seashore (Fig. 1b). Main sub-basin 1 corresponds to the Lagares river basin (Fig. 1b), which passes through the city of Vigo and drains into the Ría de Vigo estuary, at the southern end of Samil beach. Sub-basin 2 (Fig. 1b) drains into the Miñor river basin, which flows into the Ría de Vigo through the estuary of A Ramallosa. Sub-basin 3 corresponds to the Louro river basin (Fig. 1b), a tributary of the Miño river (Fig. 1a). Pond P is located just on the boundary between sub-basins 1 and 2, while ponds S and L are located at the head of sub-basin 2.

The three ponds of semi-natural origin considered in the campus (Table 1) differ in total area (size), area covered by the tree canopy, relative position along the main axis of the sub-basin, local vegetation and seasonality of the water table. Pond P is located in the upper part of the campus, at

the head of the sub-basin, pond S, in the lowermost part of the sub-basin, and pond L in the middle zone (Fig. 2). The linear distance between the two furthest ponds is 0.85 km, and the altitude difference is 71 m.

Pond P (Fig. 3a), located at 458 m asl, is artificial in origin but is fed by a natural spring at the head of the Eifonso River. The largest site studied (about 4,500 m<sup>2</sup>) has an elongated shape, and its current configuration has remained unchanged since 2005. On its margins are some riverbank trees such as *Salix alba* L., *Salix atrocinerea* Brot., *Betula alba* L., *Fraxinus excelsior* L. and *Alnus glutinosa* (L.) Gaertn. and helophytes such as *Typha angustifolia* L., *Phragmites australis* (Cav.) Trin. Former Steud. and *Juncus effusus* L., with some specimens of *Taxodium distichum* (L.) Rich. within the pond (OMA, 2020). However, this is an upland open sedimentary system without a close tree canopy that hinders the deposition of airborne material. Pond P's water table oscillates seasonally on its margins but most of the area remains permanently flooded.

Pond S (Fig. 3b), at 387 m asl, is an irregular-shaped, medium-size pond (2,500 m<sup>2</sup>) that is fed by several streams. Although it is artificial in origin, it is located in a low area with a natural tendency to flood and has maintained its current status since the year 2000. At higher levels nearby there are two settling ponds (Fig. 3b) that prevent floods and decant part of the materials dragged during rainfall periods. Furthermore, the volume dammed can be regulated by an adjustable gate, which normally remains open in winter but is closed in summer

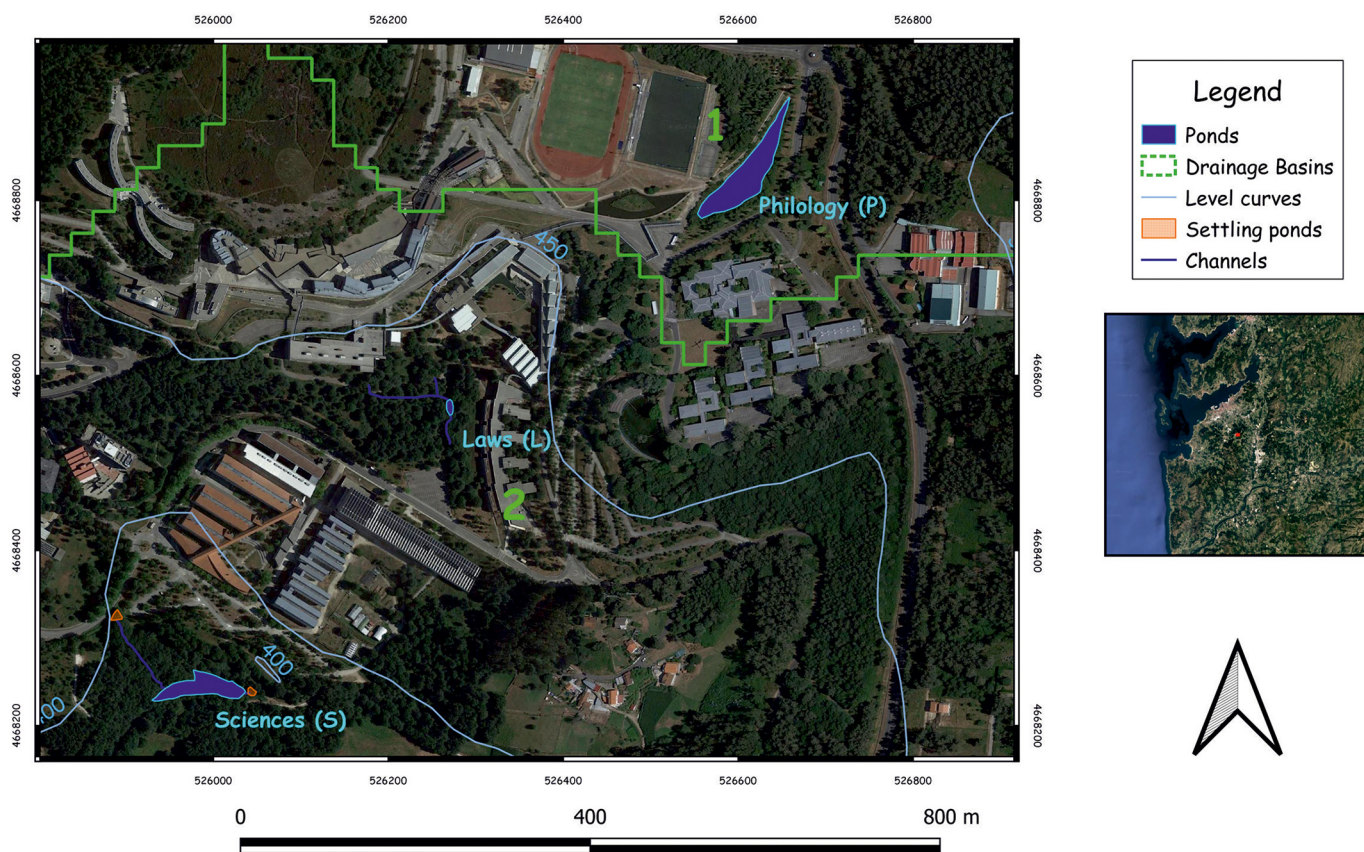


Fig. 2. Detailed aerial image of the As Lagoas-Marcosende Campus, with the situation of the three ponds (P, L, S) studied and the limits between sub-basins 1 and 2.

to preserve a minimum level of water in the lowest area, close to the gate. Therefore, the unequal distribution of annual precipitation causes the water regime in pond S to be very seasonal, with alternating periods of very high and low water levels (Fig. 3c,d). In 2019 a large part of the surface remained emerged between spring and autumn. On its margins are a variety of floating plants, helophytes and hygrophilous species, such as *Typha angustifolia* L., *Callitriche stagnalis* Scop., *Alisma plantago-aquatica* L., *Juncus effusus* L. and *Iris pseudacorus* L., and typical riparian forest trees such as *Alnus glutinosa* (L.) Gaertn., *Betula pubescens* Ehrh., *Fraxinus angustifolia* Vahl and *Salix atrocinerea* Brot. (OMA, 2020). The tree canopy covers the margins of the pond but not its central area (Table 1).

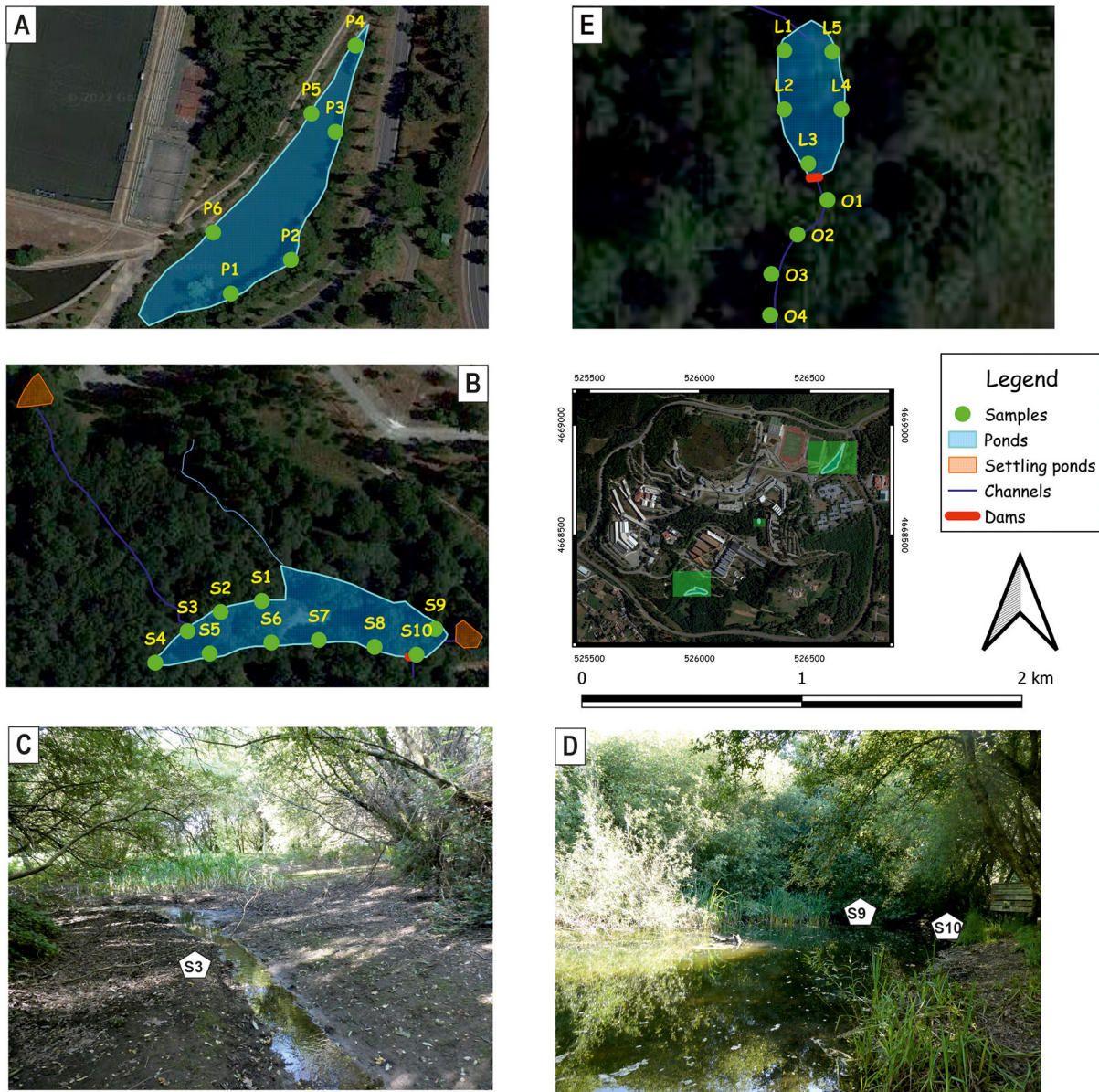
Pond L (Fig. 3e), at an altitude of 433 m asl, is also artificial in origin. It is a small pond of about 100 m<sup>2</sup> with an almost elliptic shape. It is fed by a stream from a spring (Fonte das Abelleiras) and has a dam with a spillway that connects to a drainage channel. Thus, although it

maintains a minimum stream of water continuously throughout the year, the water table remains stable and does not undergo major seasonal variations throughout the year. Pond L is surrounded by a variety of deciduous trees that extend throughout most of the sub-basin (including *Alnus glutinosa* (L.) Gaertn., *Salix atrocinerea* Brot., *Quercus robur* L., *Prunus* spp. and *Tilia* spp.), and the tree canopy practically hides the surface of the pond (Table 1). Its situation in a protected and shady area with a constant flow of water enables it to maintain a mild microclimate throughout the year, which favours the proliferation of bryophytes, ferns (*Osmunda regalis* L., *Dryopteris* spp. and *Athyrium filix-femina* (L.) Roth) and heliophytes (*Typha angustifolia* L. and *Juncus effusus* L.) on its margins, in addition to floating species (*Potamogeton natans* L.) on the water table (OMA, 2020).

The second part of this study corresponds to a reanalysis of the palaeoecological meaning of part of the pollen evidence found in a small upland lake, Laguna de la Roya in Zamora (LR, Fig. 1a), during a

Table 1  
Synthesis of the mains characteristics of the three lacustrine systems studied.

|                                    | Pond P                                                                                                                                                                                                                                                                                               | Pond S                                                                                                                                                                                                                                                                                            | Pond L                                                                                                                                                                                     |
|------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Total Surface (m <sup>2</sup> )    | 4500                                                                                                                                                                                                                                                                                                 | 2500                                                                                                                                                                                                                                                                                              | 100                                                                                                                                                                                        |
| Surface covered by tree-canopy (%) | 5                                                                                                                                                                                                                                                                                                    | 80                                                                                                                                                                                                                                                                                                | 100                                                                                                                                                                                        |
| Altitude (m a.s.l.)                | 458                                                                                                                                                                                                                                                                                                  | 387                                                                                                                                                                                                                                                                                               | 433                                                                                                                                                                                        |
| Shape                              | Irregular                                                                                                                                                                                                                                                                                            | Elongated                                                                                                                                                                                                                                                                                         | Elliptic                                                                                                                                                                                   |
| Position in the sub-basin          | High                                                                                                                                                                                                                                                                                                 | Low                                                                                                                                                                                                                                                                                               | Intermediate                                                                                                                                                                               |
| Seasonality                        | Little                                                                                                                                                                                                                                                                                               | Marked                                                                                                                                                                                                                                                                                            | None                                                                                                                                                                                       |
| Active effluent                    | None                                                                                                                                                                                                                                                                                                 | Winter and spring                                                                                                                                                                                                                                                                                 | All the year                                                                                                                                                                               |
| Local vegetation                   | <i>Salix alba</i> L., <i>Salix atrocinerea</i> Brot., <i>Betula alba</i> L., <i>Fraxinus excelsior</i> L., <i>Alnus glutinosa</i> (L.) Gaertn., <i>Typha angustifolia</i> L., <i>Phragmites australis</i> (Cav.) Trin. Former Steud., <i>Juncus effusus</i> L., <i>Taxodium distichum</i> (L.) Rich. | <i>Typha angustifolia</i> L., <i>Callitriche stagnalis</i> Scop., <i>Alisma plantago-aquatica</i> L., <i>Juncus effusus</i> L., <i>Iris pseudacorus</i> L., <i>Alnus glutinosa</i> (L.) Gaertn., <i>Betula pubescens</i> Ehrh., <i>Fraxinus angustifolia</i> Vahl, <i>Salix atrocinerea</i> Brot. | Bryophytes, <i>Osmunda regalis</i> L., <i>Dryopteris</i> spp., <i>Athyrium filix-femina</i> (L.) Roth, <i>Typha angustifolia</i> L., <i>Juncus effusus</i> L. <i>Potamogeton natans</i> L. |



**Fig. 3.** Points sampled in all the systems of sedimentation studied: a) Pond P; b) Pond S, with c) drought and d) flooded surface areas during sampling; and d) Pond L and drainage channel (O samples).

period of changing climate and local hydrological conditions (the Late Glacial to Early Holocene record) in light of the new experimental evidence provided. This lake (Fig. 1a) is located 1608 m asl, about 175 km inland and at the same latitude as the Ría de Vigo, on the highlands of the Galician Duero mountains (Muñoz Sobrino et al., 2013). The modern climate in this area corresponds to the sub-Mediterranean variant of the temperate macroclimate. The lake contains two bedrock sub-basins that connect by flooding only during the wet season, the smaller one (0.75 ha) with a depth of 1.6 m and the larger one (ca 2.5 ha) with a depth of more than 7 m. The total catchment of the lake at the Sierra Segundera highlands is about 0.21 km<sup>2</sup>, while the complete Sanabria sub-basin encompasses about 502.45 km<sup>2</sup> (Fig. 1a). Over the last decade, several multiproxy analyses have been carried out from this sequence, so various types of independent environmental data are available, including organic matter content, chironomid-inferred July air temperatures, relative and absolute abundance of local and regional pollen and freshwater algae, and planktonic and benthic diatom

composition (see Muñoz Sobrino et al., 2013; Heiri et al., 2014; Iriarte-Chiapusso et al., 2016 for details).

#### 4. Materials and methods

##### 4.1. Image analyses

A study of the whole Ría de Vigo basin was carried out using geographical information systems (QGIS software free licence; QGIS.org, 2022) from a raster layer of a digital elevation model of Galicia with a resolution of 25 m, analysing contour lines and drainage basins in the campus area (Figs. 1b, 2). The vegetation cover maps (Fig. 4) were made through a photointerpretation of a satellite image and a layer of land uses (IET, 2017). Vegetation maps in a radius of 500 m (extra-local) and 2 km (regional) from the centre of the ponds were produced to compare vegetation cover and pollen assemblages. The main vegetation units considered were “alluvial/ravine/flooded forest”, “*Pinus* and

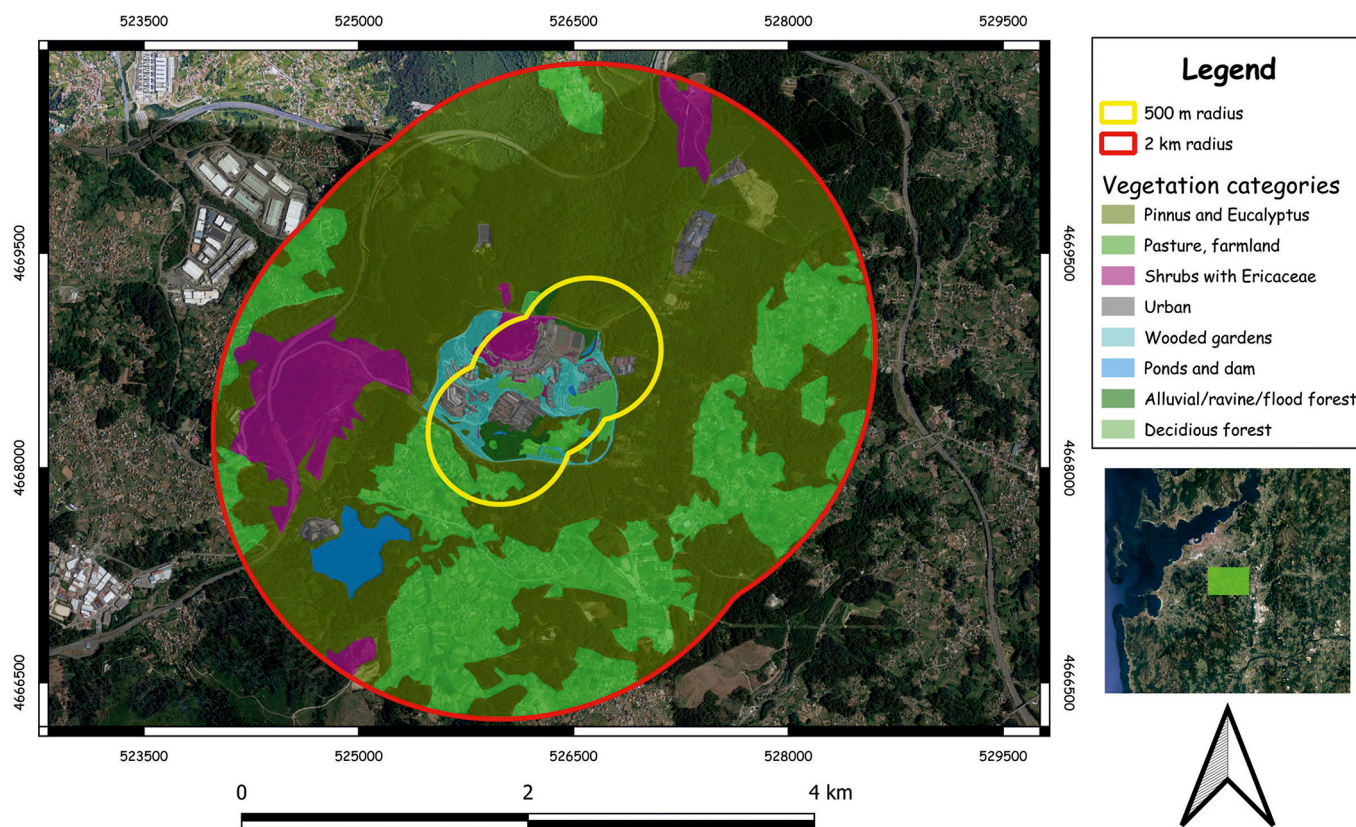


Fig. 4. Photointerpretation of the vegetation cover in a radius of <500 m and <2 km around the centre of the ponds sampled.

*Eucalyptus*" (including mixed stands), "heath and scrub", "open wooded garden areas", "mixed deciduous forest" and "pasture and farmland".

#### 4.2. Sampling methods

In August 2019, a total of 25 silty clay or sandy clay sediment samples were collected in the ponds of the As Lagoas-Marcosende Campus: 6 samples in pond P, 5 in pond L, 10 in pond S and 4 (O) from the sediment in the outlet channel of pond L. All the geolocated sampling points were distributed so that, as far as possible, they could be representative of all the margins of each pond, while the O samples were distributed at increasing distances from the spillway (Fig. 3). The samples were collected manually for both the exposed sediment samples and the surface sediment samples less than 50 cm below the water table. All 25 samples were labelled and subsequently stored in a refrigerator at 5 °C until processing.

#### 4.3. Chemical treatments and pollen identification

Before chemical treatment, all samples were dried at 80 °C for 24 h, and the dry weight and volume of each one were determined. Dry sample volumes ranged between 0.4 and 1.8 cm<sup>3</sup>, except for the three sandier samples from the drainage channel, namely O1 (2.3 cm<sup>3</sup>), O3 (3.5 cm<sup>3</sup>) and O4 (6.3 cm<sup>3</sup>). Thus, samples dry weights varied between 0.16 and 7.5 g, depending on their inorganic matter content. All samples were spiked with *Lycopodium clavatum* spores (batch 1031, Lund University, Sweden. Average concentration 20848 spores/tablet) to calculate concentrations of palynomorphs. Basic chemical treatment was carried out for the pond samples (Faegri et al., 1989; Moore et al., 1991). Accordingly, the pollen residue was extracted with KOH (10%), which facilitates the disintegration of the material and eliminates the humic acids and the larger fractions of organic matter. After basic digestion, coarse fraction (>250 µm) sediments were eliminated by sieving. Filtered samples

were repeatedly washed and centrifuged (3500 rpm), and then kept in a 50% glycerine-water mixture until observation. Finally, the slides were mounted in glycerol and analysed at 400x and 600x magnifications using a Nikon ECLIPSE 50i microscope with Nikon Ds-Fi1 photographic equipment. Mean pollen counted was 520 grains (minimum 188, maximum 1072), including at least 15 different pollen types per sample, which may create a useful dataset for our purposes (e.g. Keen et al., 2014). Various keys and pollen atlases were used to identify the pollen types: Valdés et al. (1987), Moore et al. (1991), Punt and Blackmore (1991), Reille (1995), Reille (1998) and Reille (1999).

#### 4.4. Pollen representation

TILIA 2.6.1 software (Grimm, 1990-2019) was used to process the data and prepare the pollen diagrams. The percentages of pollen and fern spores were based on a total terrestrial pollen sum, which included trees, shrubs, upland herbs and ferns; percentages of aquatic taxa were based on the total pollen sum, including all pollen and fern spores; and percentages of other non-pollen palynomorphs (microalgae, fungal remains, animal remains, etc.) were based on total organic identified remains. To calculate palynomorph concentrations, TILIA 2.6.1 software uses the formula of Faegri et al. (1989) ["total pollen = (counted pollen \* total number of added marker) / number of counted markers"], subsequently calculating the concentrations by dividing total pollen counts by the weight (g) or volume of the sample (cm<sup>3</sup>). In order to compare the pollen representation with the maps of modern vegetation more efficiently, the pollen taxa were grouped into several categories (Table 2).

#### 4.5. Numerical analyses

Firstly, all the pollen assemblages from modern sediment samples obtained in each sedimentary system studied were grouped by a

**Table 2**

Different pollen taxa grouped into the several categories of vegetation units considered, in order to compare the pollen representation with the maps of modern vegetation.

| Vegetation unit                | Pollen types included                                                                                                                                                                                                                                                                                                                                                                                                                      |
|--------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Pinus and Eucalyptus           | <i>Eucalyptus</i> , <i>Pinus</i> subgenus <i>Pinus</i>                                                                                                                                                                                                                                                                                                                                                                                     |
| Heath and Scrubs               | Ericaceae, <i>Helianthemum</i> -type, <i>Ulex</i> -type                                                                                                                                                                                                                                                                                                                                                                                    |
| Pasture and farmland           | Asteraceae_Tubuliflorae, <i>Campanula</i> -type, <i>Plantago</i> ,<br>Rosaceae, Apiaceae, <i>Urtica</i> , <i>Sinapis</i> -type,<br>Chenopodiaceae, Poaceae, <i>Galium</i> -type,<br>Asteraceae_Liguliflorae, <i>Lotus</i> , <i>Artemisia</i> , <i>Asphodelus</i> ,<br><i>Convallaria</i> -type, <i>Iris pseudacorus</i> -type, <i>Oxyria</i> -type,<br><i>Saxifraga</i> , <i>Mentha</i> -type, Caryophyllaceae, <i>Rumex acetosa</i> -type |
| Alluvial/ravine/flooded forest | <i>Alnus</i> , <i>Betula</i> , <i>Corylus</i> , <i>Fraxinus</i> , <i>Salix</i> , <i>Sambucus</i>                                                                                                                                                                                                                                                                                                                                           |
| Deciduous forest               | <i>Castanea</i> -type, <i>Quercus robur</i> -type                                                                                                                                                                                                                                                                                                                                                                                          |
| Open wooded garden areas       | <i>Acacia</i> , <i>Tilia</i> , <i>Olea europaea</i> , <i>Populus</i>                                                                                                                                                                                                                                                                                                                                                                       |
| Ponds and dams                 | <i>Callitriche</i> , <i>Equisetum</i> , <i>Typha latifolia</i> -type, <i>Alisma</i> -type,<br>Bryophyte spores, <i>Potamogeton</i> , Cyperaceae                                                                                                                                                                                                                                                                                            |
| Urban areas                    | None                                                                                                                                                                                                                                                                                                                                                                                                                                       |

constrained incremental sum of squares (CONISS) cluster analysis (based on Edwards & Cavalli-Sforzas chord distance) in order to get a quick picture of the possible differences between samples from the same site (Fig. 5). A similar analysis was performed for the whole set of samples studied in order to understand possible differences between samples from different sites (Fig. 6a).

Secondly, a detrended correspondence analysis (DCA) was conducted on square root-transformed pollen percentage data. DCA Axis 1 length-of-gradient was 1.06 standard deviation units of turnover, so it was suitable to use principal component analysis (PCA) to corroborate the CONISS grouping and determine the taxa to which differences between the samples were due (Legendre and Birks, 2012). For DCA and PCA analyses, only the most relevant taxa were included, i.e. those representing more than 1% in at least one sample. Then, percentages were recalculated based on the total number of remains considered, and a square root transformation was applied to reduce the asymmetry in the data distribution (Legendre and Birks, 2012).

The descriptive statistic Omega squared ( $\omega^2$ ) was calculated (Table S1) to quantify the strength of the relationships between the qualitative explanatory independent variable (type of sedimentary system) and the quantitative response of the dependent variable (pollen abundance in each sedimentary system). Intra-class correlation

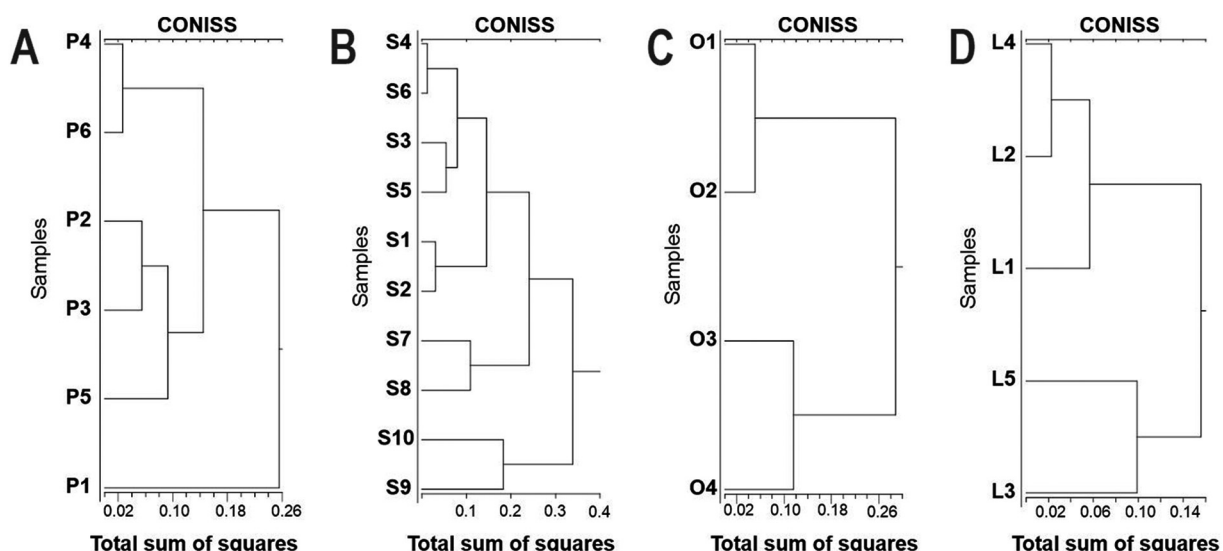
coefficients (Table S1) were also used to describe how strongly the different samples from the same pond resembled each other. The main differences in the abundance of selected pollen types identified as the most dissimilar between sites or between samples taken at the same site are represented in boxplots (Fig. 7). To determine whether these differences were significant, several types of test (the Levene test, the Welch F test, one-way ANOVA, the Kruskal-Wallis test for equal medians, the Tukey pairwise test, the Mann-Whitney pairwise test and the Dunn post hoc test) were applied both to the percentage and to the pollen concentration data (Tables S1, S2, S3). The DCA (not shown), PCA (Fig. 8), descriptive statistics, ANOVAs, and other several-sample tests (Tables S1, S2, S3) were performed using the PAST software (Hammer et al., 2001), and the boxplots (Fig. 7) of selected pollen types were created using the data analysis package implemented in Microsoft Excel.

## 5. Results and interpretation

### 5.1. Vegetation cover vs pollen percentages

The total weight of each unit of vegetation (expressed as a percentage of the surface covered with respect to the total surface) varies considerably depending on whether extra-local (<500 m) or regional (<2 km) vegetation was considered (Fig. 9). Thus, landscape units such as “urban areas” (20%), “open wooded garden areas” (14.6%), “deciduous forest” (5.1%) and “alluvial/ravine/flooded forest” (7.3%) are relevant in a radius of less than 500 m from the centre of the ponds but decay at a regional scale (<2 km), where they only represent 3%, 2.2%, 0.7% and 0.8%, respectively. Alternatively, extra-local “pasture and farmland” (12.4%) and “*Pinus* and *Eucalyptus*” (33.65%) types are clearly underrepresented because at a regional range they respectively represent 24.42% and 60.18% of the total vegetation. The last category considered, “heath and scrubs” show quite similar results at both the extra-local (6.38%) and regional (7.39%) scales.

On the other hand, landscape units without a clear pollen signal (i.e. “urban areas” and “open wooded garden areas”) are inevitably underrepresented in the pollen records, while the importance of “ponds and dams” is artificially emphasized by the abundance of local pollen from aquatics (Fig. 9). Furthermore, the capacity of the averaged pollen records at each site to reflect both the extra-local and the regional vegetation cover varies depending on the systems of sedimentation and the types of vegetation considered (Fig. 9). Average values obtained from



**Fig. 5.** Results of the cluster analyses corresponding to the samples studied in each sedimentary system. a) Pond P samples; b) Pond S samples; c) O samples; d) Pond L samples.





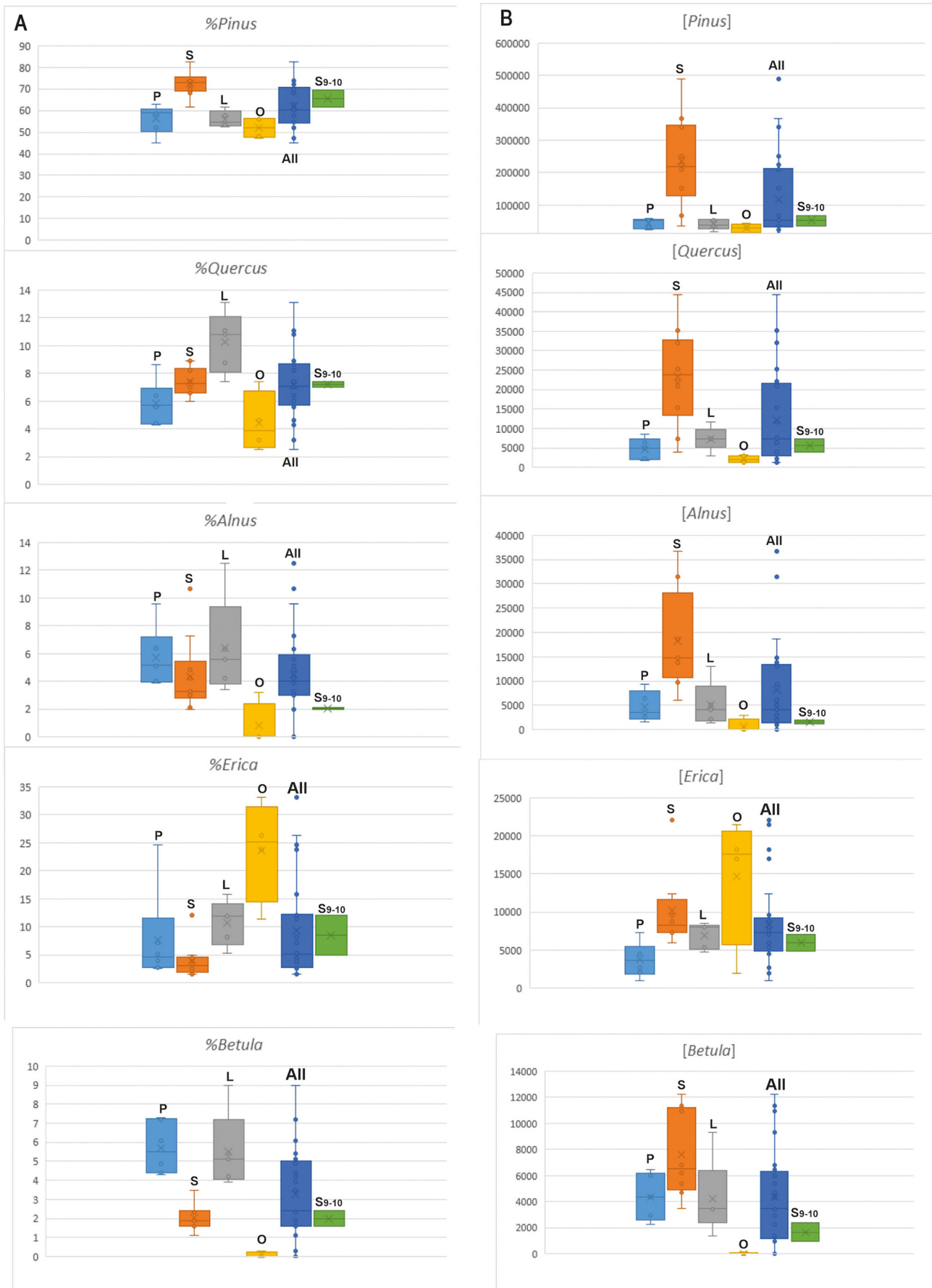
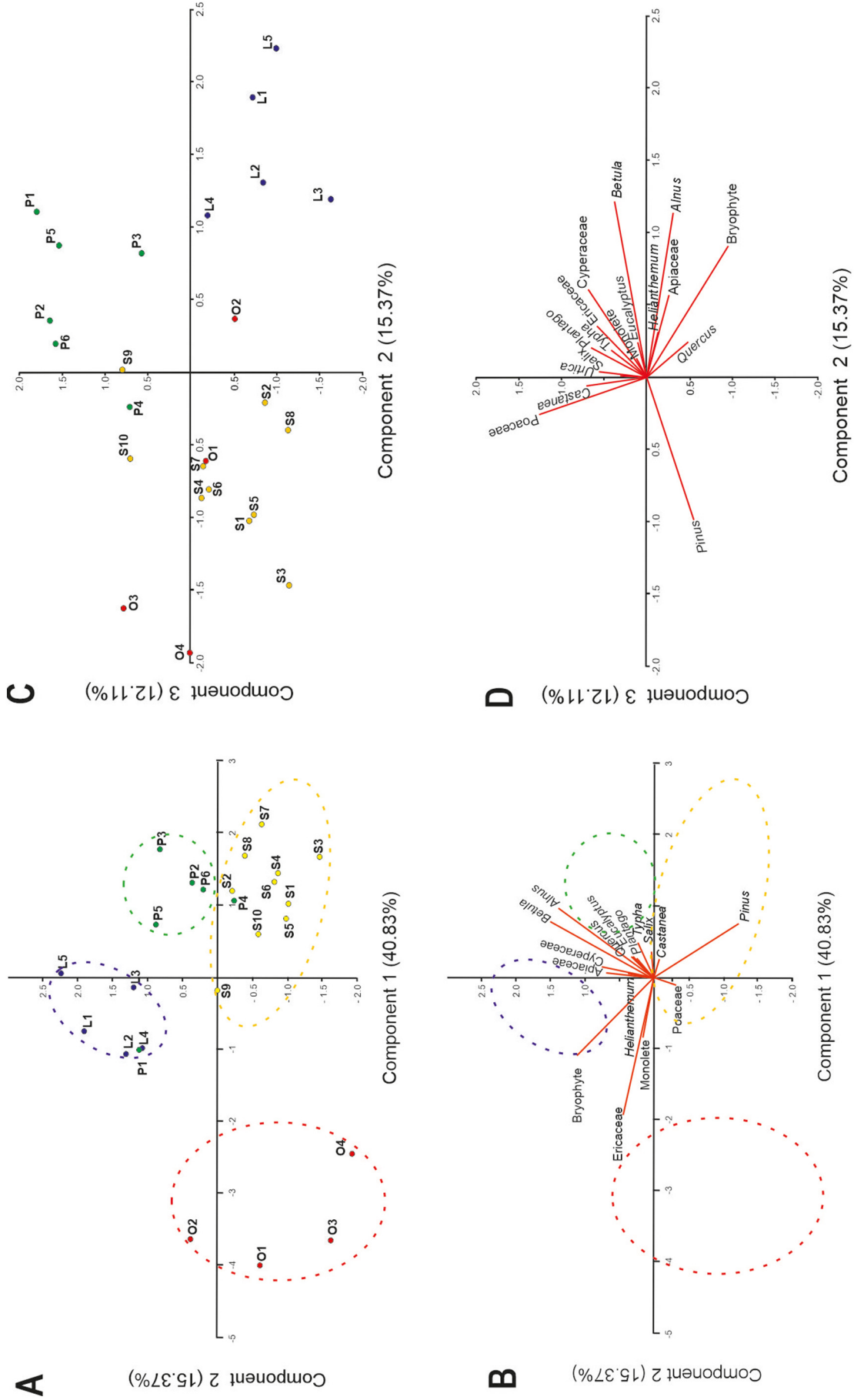
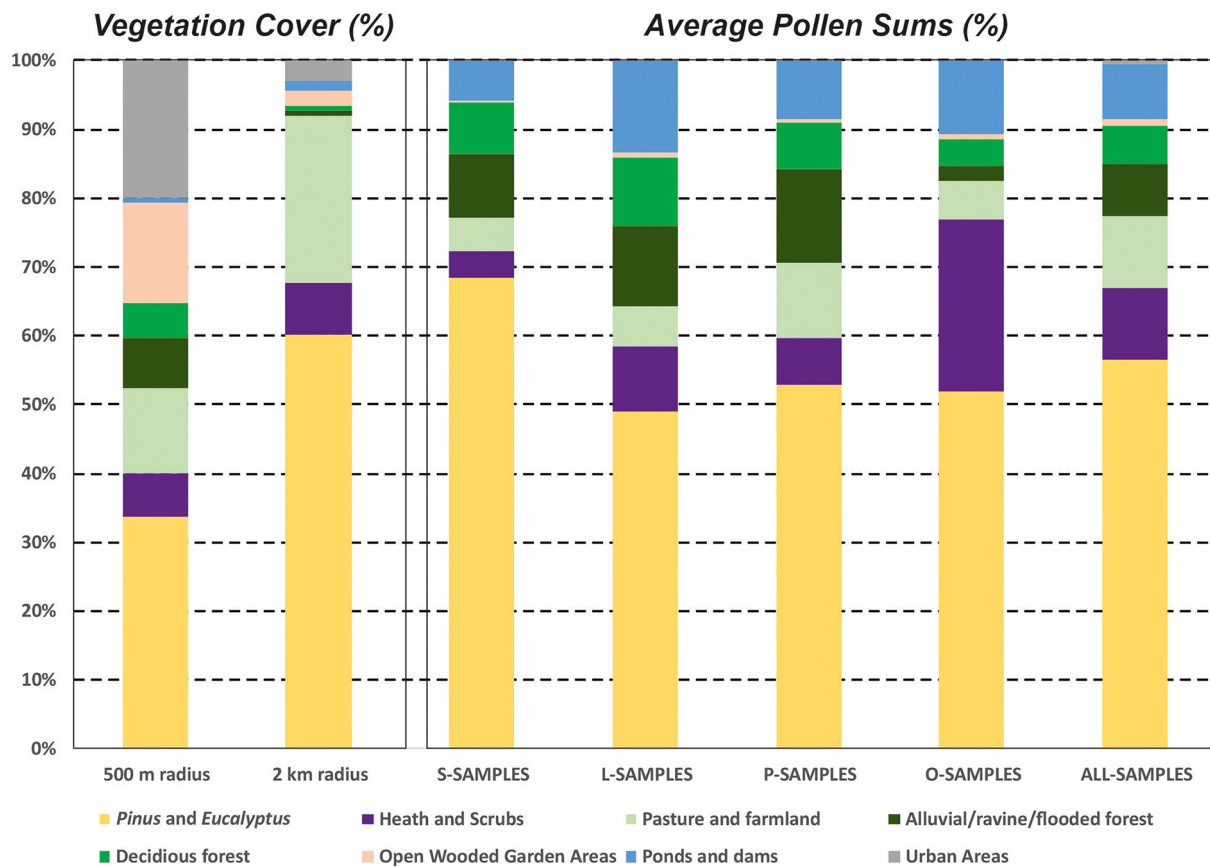


Fig. 7. Box-and-whisker plots for percentage (a) and concentration (b) data obtained for selected pollen types in the sedimentary systems studied.



**Fig. 8.** Principal component analysis describing the relative position of all the samples studied (a) and the most relevant taxa (b) in the bi-dimensional space formed by Axis-1 and Axis-2; and also describing the relative position of all the samples (c) and the most relevant taxa (d) in the two-dimensional space formed by Axis-2 and Axis-3.



**Fig. 9.** Comparison between the main extra-local (<500 m) and regional (<2 km) types of vegetation cover (see text for details) and the averaged pollen percentages representing these types of vegetation (see text for details) in each sedimentary system studied, and also the pollen percentages corresponding to each type of vegetation as averaged for all the samples studied.

Pond S samples fit quite well with the extra-local values for “deciduous forest” (7.36%) and “alluvial/ravine/flooded forest” (9.01%). However, they minimize the importance of some open vegetation units, “pasture and farmland” (4.67%) and “heaths and scrubs” (3.85%), and considerably overestimate the importance of “*Pinus and Eucalyptus*” (66.74%). Average values from Pond L samples overestimate the importance of “heaths and scrubs” (9.21%), “deciduous forest” (9.61%) and “alluvial/ravine/flooded forest” (11.43%), but underestimate “pasture and farmland” (5.43%) and the regional “*Pinus and Eucalyptus*” (47.31%). Average values from Pond P samples agree closely with the extra-local vegetation cover in the case of “deciduous forest” (6.49%), “heaths and scrubs” (6.48%) and “*Pinus and Eucalyptus*” (51.68%), but overestimate “alluvial/ravine/flooded forest” (13.38%). Finally, average values from O samples clearly overestimate the extra-local and regional importance of “heaths and scrubs” (25.14%). Ultimately, the best fit between the vegetation categories considered at extra-local and regional levels and the pollen percentages results from the averaged pollen values of the entire set of samples studied, regardless of the sedimentary system from which they come (Fig. 9).

## 5.2. Variability of samples in each sedimentary system

Cluster analyses indicate that all the samples obtained in Pond L are very similar to each other (Fig. 5). Furthermore, dissimilarity between samples O obtained in the channel draining Pond L is low or intermediate (Fig. 5), the two samples located closest to the spillway (O1 and O2) being the most similar to each other and somewhat different from the other pair (O3 and O4). Pond P samples show intermediate differences between P1 and the rest. Finally, the largest intra-pond differences

correspond to the Pond S samples, in which the pair S9 and S10 is quite different from the others (Fig. 5).

## 5.3. Comparative analysis of the set of modern pollen assemblages

The results of the cluster analysis for all the samples studied differentiate two main clades that clearly separate one group of samples (O1 to O4) from the others. That second clade comprises three subclades including 1) samples S1 to S8; 2) samples S9, S10 and P2 to P5; and 3) samples P1 and L1 to L5.

The percentages of the anemophilous *Pinus* pollen (very abundantly produced, saccate and airborne-transported) range between 83% and 45% of the total pollen identified in each sample, and they are thus dominant in all the samples studied. However, *Pinus* percentages are particularly high (>59%) in most of the S and P samples, except in samples P5 (52%) and P1 (45%) (Fig. 6a). Ericaceae is the second most represented taxon, with high percentages (33%–11%) in all the samples taken in the drainage channel (O1 to O4), in most of the Pond L samples (L1, L2, L4) and also in samples S9 and P1. *Quercus robur*-type (<13%) and *Alnus* (<12%) also appear in all the samples studied, but their percentages are higher in all the Pond L samples and in most of the Pond S samples, while *Betula* (<10%) is more abundant in the samples taken in ponds L and P. Alternatively, Poaceae are high in samples O3, O4, S9 and S10; and Monolete spores peak (>10%) in samples O1 and O2 (Fig. 6a).

Intra-class correlation coefficients calculated for percentages of some selected pollen types in each sedimentary system studied are very high (>0.75) for *Betula* and *Pinus* and high (>0.6) for *Quercus* and Ericaceae, but strong relationships ( $\omega^2 > 0.7$ ) are only found

between the pollen percentages of *Betula* and *Pinus* and the “system of sedimentation” variable (Table S1).

The total pollen concentration varies considerably between sites, and also between some samples taken from the same pond (Fig. 6b). Accordingly, the greatest pollen concentrations are  $>6 \times 10^5$  grains/cm<sup>3</sup> in the S1 to S8 group of samples, i.e. more than 30 times greater ( $<2 \times 10^4$  grains/cm<sup>3</sup>) than the total pollen concentrations recorded in the rest of the samples studied, and also six times greater than in the two other samples (S9 and S10;  $<10^5$  grains/cm<sup>3</sup>) taken in Pond S (Fig. 6b).

#### 5.4. Principal component analysis

The first two axes of the PCA explain in total 55.67% of the variation in the pollen dataset (Axis 1, 40.83%; Axis 2, 15.37%; Fig. 8ab). Total variation explained is 67.78% with the incorporation of Axis 3, which represented 12.11% of the variation (Fig. 8cd). In general, the PCA results corroborate the CONISS classification and also confirm that the main taxa explaining the differences between samples are *Pinus*, Ericaceae, a number of deciduous trees (*Alnus*, *Betula*, *Quercus*, *Salix* and *Castanea*) and the local aquatic/hygrophilous vegetation of each pond (Fig. 8b). Principal taxa positively contributing to Axis 1 are the most common anemophilous trees in the area (*Alnus*, *Betula*, *Pinus*, *Quercus*, *Salix* and *Castanea*), while only four taxa (Ericaceae, Monoete spores, Bryophyte spores and Poaceae) show negative scores. Therefore, Axis 1 show a gradient that may be ultimately related to the size of the pond, its exposed surface and its position in the basin, because most of the samples taken in the two open larger ponds (P and S samples) show positive scores (i.e. pollen in the sediment was mainly airborne), whereas both samples in the small Pond L, fed by water flows and covered by a close tree canopy, and samples O1 to O4 in its drainage channel clearly show Axis-1 negative scores. Finally, samples L3, L5 and S9 show values close to 0 for Axis 1, suggesting a mixed pollen contribution (i.e. airborne but also provided by means of water flows).

Principal taxa positively contributing to Axis 2 are mainly riparian, hygrophilous or aquatic (*Betula*, *Alnus*, Bryophyte spores, Apiaceae and Cyperaceae), while most negative scores are for two anemophilous types, *Pinus* and Poaceae. Axis 2 separates most of samples P and L (positive scores) from most of samples S and O (negative values), with sample S9 (on the fringe between the permanent and temporal water table, Fig. 3d) scoring 0. Therefore, Axis 2 represents a gradient of the height of the water table from high (positive scores) to low (negative scores) levels. Furthermore, in the two-dimensional space formed by Axis 2 and Axis 3 (Fig. 8d) *Castanea* and Poaceae contribute positively and *Pinus* contributes negatively to Axis 3, suggesting that percentages of chestnut and grass pollen increase during the wet periods when the water table is high, but that the sediment is enriched in *Pinus* pollen during the dry periods when the water table is low.

## 6. Discussion

### 6.1. Factors explaining unequal pollen records from nearby sedimentary systems

As a result of the experimental design pond size explains a considerable part of the total variance (until 40.83%), thus confirming the generally accepted assumption that larger lakes can generally collect pollen from a wider source area (e.g. Jacobson and Bradshaw, 1981) and large sites may therefore be more useful for estimating the regional vegetation composition (e.g. Sugita, 2007a). However, other differences in pollen assemblages not related to pond size are found between sites and may have important implications for the reconstruction of the extra-local and regional vegetation.

The average percentages of all the pollen assemblages from modern sediment samples analysed allow a fairly suitable reconstruction of the main extra-local ( $<500$  m) and regional ( $<2$  km) vegetation units around the set of sedimentary systems studied (Fig. 9). However, the

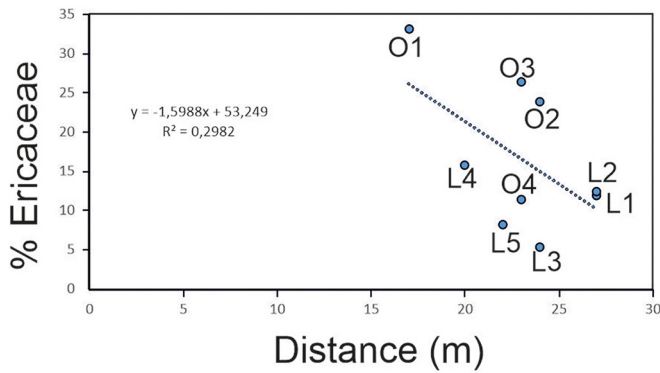
results are considerably worse for the average sample in each sedimentary system (Fig. 9), and there are even major differences between samples taken from the same system (Fig. 7). Both CONISS (Fig. 6) and PCA (Fig. 8a) group together most of the samples taken from the same sedimentary system (mostly because of the weight of the local pollen component), but there are clear exceptions: samples S9 and S10 are quite similar to most of the Pond P samples, but sample P1 is clustered with the Pond L samples.

The main regional taxa differentiating samples along the PCA Axis 1 are *Pinus*, *Alnus* and *Betula* in the positive range and Ericaceae in the negative range (Fig. 8b). One-way ANOVA tests confirm statistically significant differences between the mean percentages of *Pinus*, *Alnus* and Ericaceae found in the sedimentary systems (Table S2). According to the Levene test, the variable *Betula* lack homoscedasticity, but the Welch F test and the Kruskal–Wallis test also suggest statistically significant differences for the distribution of birch pollen percentages in the systems studied (Table S1).

In relation to *Pinus* percentages, all the pairwise tests (Tukey, Mann–Whitney and Dunn’s post hoc) reveal significant differences between the S samples and the others (Table S2). Furthermore, the Tukey pairwise test (which tolerates type I errors) indicate that Ericaceae percentages are significantly different in the O samples from the samples taken in ponds P, S and L, but both the Mann–Whitney test (testing whether one distribution is stochastically greater than the other) and the Dunn post hoc test (more rigorous but with lower statistical power) pinpoint that significant differences only exist between the S–L, S–O and P–O samples (Table S2). *Alnus* percentages are different between the L–O and P–O samples according to the Tukey and Dunn post hoc tests, while the Mann–Whitney pairwise test also reveals significant differences between S–O samples (Table S2). Finally, *Betula* percentages are also different between L–O, P–O, S–L and S–P samples according to the Tukey pairwise and Dunn post hoc tests; and the Mann–Whitney test also found differences between S–O samples (Table S2).

Taxa positively contributing to PCA Axis-1 (*Pinus*, *Alnus* and *Betula*) are all anemophilous species capable of producing large amounts of airborne pollen. Alternatively, the majority of heath species are low-growing entomophilous plants that release their poorly dispersed pollen in tetrads. However, some species with exerted stamens (e.g. *Calluna vulgaris* (L.) Hull., *Erica umbellata* L., *E. vagans* L., *E. erigena* R. Ross and *E. australis* L.) can have some anemophilous pollination and often have better pollen dispersal (Huntley and Birks, 1983). In our study, the association of Ericaceae with other local vegetation (bryophytes and ferns) characteristic of Pond L and the O samples taken in its drainage channel suggests that the majority of the heath pollen contribution in these sedimentary systems comes through water flows. Furthermore, Ericaceae percentages are significantly higher in the drainage channel (O samples) than in Pond L, and these differences cannot be directly attributed to a shorter distance from the nearest heath stands (Fig. 10). Finally, pollen records from Pond L and its drainage channel are different from those obtained in ponds P and S, and the main factors explaining the variances are the greater size and the lack of a close tree canopy of ponds P and S, in addition to the higher contribution of heaths in Pond L and also in the O samples.

Thus, the experimental evidence suggests that Ericaceae pollen is more intensely transported by water flows than other pollen types, probably because of the better buoyancy and hydrodynamic characteristics of its tetrads, which subsequently accumulate on the margins of the drainage channel. Brown et al. (2007) argue that fluvial (waterborne) pollen transport is the most important pollen source into most lakes and near-shore marine sediments, and point out that peaks of Ericaceae pollen found in surface sediment from fluvial systems can be related to flood events. Moreover, a preferential ability of tetrads to be transported by water could explain why *Erica* pollen range between 10% and 20% in contemporaneous full-marine sediments at the southern margin of the Cíes Islands in Ría de Vigo (Fig. 1b, Muñoz Sobrino et al., 2016), though there is currently no local heathland on the islands



**Fig. 10.** Percentages of Ericaceae of each sample taken in Pond L (L samples) and its drainage channel (O samples) in relation to the distance to the nearest heather stands around them.

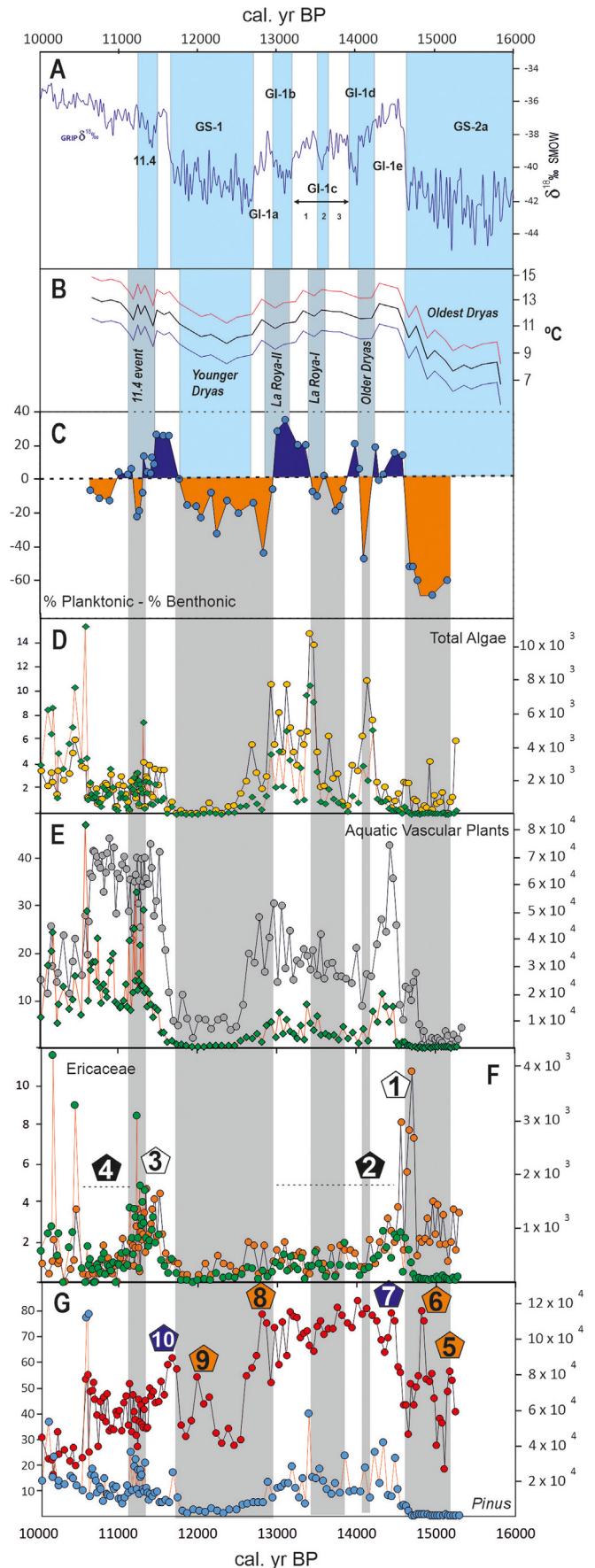
(nor was there throughout the 20th century, see *Losa España, 1944*) and the closest heaths in the continent are more than 5 km distant at Cape Home (*Fig. 1b*).

PCA Axis-2 explaining nearly 16% of the total variance, separates samples obtained at sites with an almost permanent water table (P and L samples) from other groups of samples (most of the S and O samples) taken in extremely seasonal systems of sedimentation (*Fig. 8a*). The highest positive scores correspond to hygrophilous taxa (*Betula, Alnus, Apiaceae* and *Cyperaceae*) and the negative scores mainly include *Pinus* and *Poaceae*, in addition to *Castanea*. PCA Axis-3 representing 12.11% of the variance indicates a negative contribution of bryophytes, *Pinus, Quercus, Alnus, Apiaceae* and *Helianthemum* and positive contribution of *Poaceae* and *Castanea*, for the water flow-transported Ericaceae, for some hygrophilous taxa (*Salix, Cyperaceae, Typha, Betula*) and for most of the nitrophilous taxa (*Urtica, Plantago*). These results suggest that the main factor explaining the high percentages and concentrations of *Pinus* found in the samples taken in Pond S, which are significantly higher than those found at the other sites analysed (Tables S2, S3), independently of their total size and the area covered by the tree canopy, is the desiccation of a large part of the pond surface for long periods. It is noteworthy that *Pinus* percentages and concentrations for the two S samples with a permanent water table (S9 and S10) are consistently lower than those recorded in the rest of the S samples and more similar to those found in Pond P (*Fig. 6*). This finding suggests that the saccate *Pinus* pollen tends to float in the water and get partially lost in the effluents, but tends to concentrate when the water table falls and the sediment is directly exposed to pollen rain.

**6.2. Implications for the interpretation of palaeoecological pollen data in small lakes**

It is expected that the new experimental evidence presented above may be useful for re-evaluating some of the classical interpretations of pollen data obtained from small lakes in the Atlantic and circum-Mediterranean areas, including the representation of heathland and pinewoods. One of the outstanding inferences of the experimental study carried out in different types of upland ponds is that the interpretation of the importance of heathland in landscape using pollen data may be magnified by the transport of tetrads through water flows and their accumulation in the basin.

European Atlantic heathlands require humid oceanic climates and are limited by cold temperatures (thermicity) and summer droughts (*Loidi et al., 2010*). After the end of the last glacial period (<11,650 cal yr BP), a general expansion of broadleaf deciduous pollen occurred in NW Iberia, partially replacing heathlands and other open habitats (e.g. *Iriarte-Chiapusso et al., 2016*). However, heathland extent peaked asynchronously in different areas of western Europe from the Bronze



age onwards (e.g. van der Knaap and van Leeuwen, 1997; Webb, 1998; Ramil-Rego et al., 1998; Karg, 2008; Nielsen and van Ongaard, 2010; Connor et al., 2012) and has been attributed to a combination of changing climates and the transformation of agro-systems (Fagúndez, 2013).

In NW Iberia most of the Ericaceae pollen expansions occurring during the Late Holocene have been recorded in small upland lakes (Fig. 1a): e.g. Arroyo de As Lamas (Maldonado Ruíz, 1994); Laguna de la Roya and Lago de Ajo (Allen et al., 1996); Lagoa de Marinho (Ramil-Rego et al., 1998); Porto Ancares and A Golada (Muñoz Sobrino et al., 1997); Lagoa de Lucena (Muñoz Sobrino et al., 2001); Pena Velosa (Muñoz Sobrino et al., 2012a); and Lago Ausente (Morales-Molino et al., 2022). Owing to the limited capacities for airborne pollen dispersion of most of the Ericaceae these expansions most probably directly reflect the heathland colonizing the spaces situated above the lakes.

Pollen percentages in palaeoecological records corresponding to upland taxa are interrelated because they represent proportional values. Furthermore, pollen percentages from aquatic vascular plants depend on changing environmental conditions: mainly precipitation, temperature and duration of the ice-free season but also total pollen abundance. Other independent proxies such as chironomids and diatoms may be useful for respectively evaluating changes in temperature and water-table regimes. Particularly, periphytic (benthonic) diatoms can indicate both low water levels and a good local development of aquatic vegetation, but dominance of planktonic diatoms may be unequivocally related to high water tables.

Laguna de la Roya (Fig. 1a), a small (0.03 km<sup>2</sup>) lake at a height of 1608 m, placed on a small upland sub-basin (0.21 km<sup>2</sup>) that dominates the large Sanabria lowlands (>500 km<sup>2</sup>, <1000 m high) is a good option for this analysis, because the high-resolution pollen record of this lake can be used to monitor the changing local, extra-local and regional pollen contributions recorded under different environmental scenarios, which besides may be independently reconstructed by using the other multiproxy data available (Heiri et al., 2014).

High-resolution multiproxy data from Laguna de la Roya (Fig. 11) suggest that the same effect found in our experimental design (i.e. pollen overrepresentation in the sediment of the extra-local heaths surrounding the basin) occurred during the two wetter phases recorded during the Late Glacial-Holocene transition: the beginning of the Late Glacial Interstadial at ca. 14,700 cal yr BP (1 in Fig. 11f); and the transition between the Younger Dryas and the early Holocene at ca. 11,500 cal yr BP (3 in Fig. 11f). Multiproxy evidence indicates that a longer ice-free season occurred in Laguna de la Roya after 14,700 cal yr BP and is supported by the increase in chironomid-inferred July temperatures. At this moment (1 in Fig. 11f), the productivity in the water column increased, as evidenced by a rise in total diatom accumulation rates and an increase in planktonic diatoms, in addition to green algae (*Pediastrum*, *Botryococcus*, *Zygnemataceae*; Fig. 11d) and macrophytes (*Alisma*

*plantago-aquatica*, *Ranunculus*-type, *Equisetum*, *Isoëtes*, Fig. 11e). A similar tendency (a rise of chironomid-inferred July temperatures and increases in planktonic diatoms, total diatom accumulation and vascular aquatic plants) is also observed (3 in Fig. 11f) at about 11,700 cal yr BP (Muñoz Sobrino et al., 2013; Heiri et al., 2014). Therefore, we suggest that the two peaks in Ericaceae pollen percentages (and to a lesser extent also in Ericaceae pollen accumulation rates) were forced by the flows and runoff filling the catchment at the beginning of the two wetter phases recorded (Fig. 11f). Alternatively, the decrease in Ericaceae percentages during the two following warmer stages (phases 2 and 4 in Fig. 11f) may be at least partially connected to the great buoyancy capacity of tetrads, which promoted their preferential exit from the sedimentation system when the water level was high and the effluents were active.

During the Oldest Dryas (before ca 14,700 cal yr BP) and during the Younger Dryas (12,750–11,700 cal yr BP), the lake was characterized by a low aquatic productivity, as shown by the domain of periphytic diatoms and the scarcity of local aquatic vegetation and sedimentary organic matter, while the estimated summer temperatures were low (<9 °C and 11 °C–9 °C, respectively; see Fig. 11b), and the tree-line was situated below the catchment of Laguna de la Roya (Muñoz Sobrino et al., 2013). Consequently, several of the *Pinus* pollen peaks (5, 6 and 9 in Fig. 11g) found during the coldest and driest Late Glacial stages (Oldest Dryas and Younger Dryas) can be related to the stages of lowest water table recorded in the basin, or occurred during its emptying (8 in Fig. 11g). Thus, the environmental meaning of these *Pinus* maxima seems to be completely different from that of other peaks (7 and 10 in Fig. 11g), representing the rise of the tree-line (mainly pine-woods) as the result of the climatic warming and the pine developing above the catchment of Laguna de la Roya (Allen et al., 1996; Muñoz Sobrino et al., 2004, 2013). Therefore, a good practice for improving the interpretation of the percentages of Ericaceae and *Pinus* in small upland lakes with fluctuating water levels from the Atlantic or circum-Mediterranean regions would be to analyse any relationships they may have with the local aquatic flora dynamics or, preferably, with other independent water-level indicators (e.g. diatoms).

## 7. Conclusions

An experimental study carried out in different types of upland ponds in the same basin confirms that pond size may be directly related to the source area and explains a great proportion of the variability observed in the pollen records. Moreover, it is concluded that the average pollen percentages of all the assemblages obtained from the set of modern sediment samples analysed can be used to make a fairly suitable reconstruction of the main extra-local (<500 m) and regional (<2 km) vegetation units around the sedimentary systems studied. However, there are important differences between the average samples obtained in each sedimentary system, and also between some samples taken from the same sedimentary system. The main factors explaining these differences are the abundance of anemophilous pollen (directly related to the size of the pond), the pond's tree canopy (inversely related to the abundance of anemophilous pollen) and the seasonality of the water table, which strongly determines the percentages of extra-local Ericaceae and regional *Pinus* and also the *Pinus* and total pollen concentrations. The great buoyancy capacity of tetrads and saccate pollen can reduce the representation of these pollen types in sedimentary systems with flowing waters. Regional airborne *Pinus* pollen can also be overrepresented in small lakes characterized by strongly seasonally fluctuating water levels. In light of this experimental evidence, the high-resolution multiproxy palaeoecological record obtained from an upland small lake in the NW Iberian Peninsula was re-evaluated, and it is concluded that the interpretation of the importance of extra-local heathland or regional pinewoods on landscape using pollen data may be magnified during rainy periods by the transport of tetrads and saccate pollen through water flows and their accumulation in the basin. Alternatively, the

**Fig. 11.** Re-evaluation of some of the high-resolution multiproxy data from Laguna de la Roya (LR) (Muñoz Sobrino et al., 2013; Heiri et al., 2014). a) The main Late Glacial INTIMATE climatic episodes and events (Blockley et al., 2012) as compared with the climatic and environmental reconstructions obtained from the Greenland Ice Core Project oxygen isotope record, following the GICC05 time scale presented by Vinther et al. (2006) and Rasmussen et al. (2006). b) Late Glacial chironomid-inferred July temperatures (°C) obtained at LR (including the estimated standard error of prediction). c) Differences between the percentages of planktonic and benthonic diatoms recorded in the sediment from LR. Blue intervals represent local high water-level stages (see text). d) Percentages (yellow circles) and accumulation rates (green diamonds) of the total green algae and cyanobacteria evidence found at LR. e) Variations of percentages (grey circles) and accumulation rates (green diamonds) of the aquatic vascular plant pollen sum at LR. f) Variations in percentages (orange circles) and accumulation rates (green circles) of Ericaceae pollen at LR. g) Variations in percentages (red circles) and accumulation rates (blue circles) of *Pinus* pollen at LR. Pollen/algae accumulation rates are expressed as grains per cm<sup>2</sup> yr<sup>-1</sup>. Phases 1 and 3 are interpreted as rainy periods when flows and runoff fill the LR catchment. Also, lake effluents were probably active during phases 2 and 4. *Pinus* peaks 7 and 10 are interpreted as representing pinewoods placed near/around the catchment during a relatively warm period. They are different to *Pinus* peaks 5, 6, 8 and 9, which correspond to cold events and were probably magnified by low water tables (see text).

sediment can be depleted of pollen types with enhanced buoyancy capacities (such as tetrads and saccate pollen) when the water level is high and the effluents are active. These effects may also be important in other sedimentary systems, and are probably connected to the long-distance transport and overrepresentation of heath and pine pollen usually observed in fluvio-marine sedimentary systems (e.g. Brown et al., 2007; Rodríguez-Gallego et al., 2012; García-Moreiras et al., 2015; Muñoz Sobrino et al., 2016). Therefore, the new experimental evidence may be useful for re-evaluating the environmental meaning of pollen evidence found during the Late Glacial and Holocene in seasonal upland lakes, and also for interpreting pollen records obtained in fluvio-marine systems, including sediment from tidal coastal lagoons with oscillating water tables.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2022.104765>.

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